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WEST COLOMBIAN BIOGEOGRAPHY. NOTES ON *HELICONIUS HECALESIA* AND *H. SAPHO* (NYMPHALIDAE)

KEITH S. BROWN, JR.[1,2] AND WOODRUFF W. BENSON[1,2]

The western Cordillera of Colombia (Fig. 1) is a presently imperfect barrier for the dispersion of many butterflies which inhabit the tropical forests on its inner and outer (seaward) slopes. Several well-differentiated subspecies from the central valleys and the Pacific coastal regions of Colombia are known to meet locally and hybridize near lower passes (~1500 m) in the mountain chain between these warmer areas. Some of these, long considered as good species, have been able to overcome evolutionary barriers against interfertilization and form mixed populations. A good example of this is in the ithomiines *Hypothyris euclea caldasensis* Fox (Pacific slopes) and *H. e. philetaera* (Hewitson) (central valleys), which mix in various localities over a broad region from central Panamá south to Nariño in extreme southwestern Colombia, producing polymorphic populations which have given rise to at least four additional names, representing recombinants of the two parent color-patterns ("micheneri" Fox, "nemea" (Weymer), and "bifasciata" (Neustetter) ≅ "neustetteri" Real) (cf. Fox & Real, 1971). A much more restricted mixing takes place between *Heliconius clysonymus clysonymus* Latreille (central valleys) and *H. c. hygiana* (Hewitson) (western Ecuador), which meet in sparse populations near Queremal and Lago Calima, west of Cali, Colombia, forming unusual polymorphic populations with recently described forms (Holzinger & Holzinger, 1970; Brown & Mielke, 1972). *Heliconius cydno weymeri* Staudinger ranges from the upper Cauca Valley into these same areas and the Dagua

[1] Departamento de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, C.P. 1170, Campinas, São Paulo 13.100, Brazil (present address of both authors).
[2] Centro de Pesquisas de Produtos Naturais, I.C.B., C.C.M., Universidade Federal do Rio de Janeiro, Ilha do Fundão, Rio de Janeiro ZC-32, Brazil.

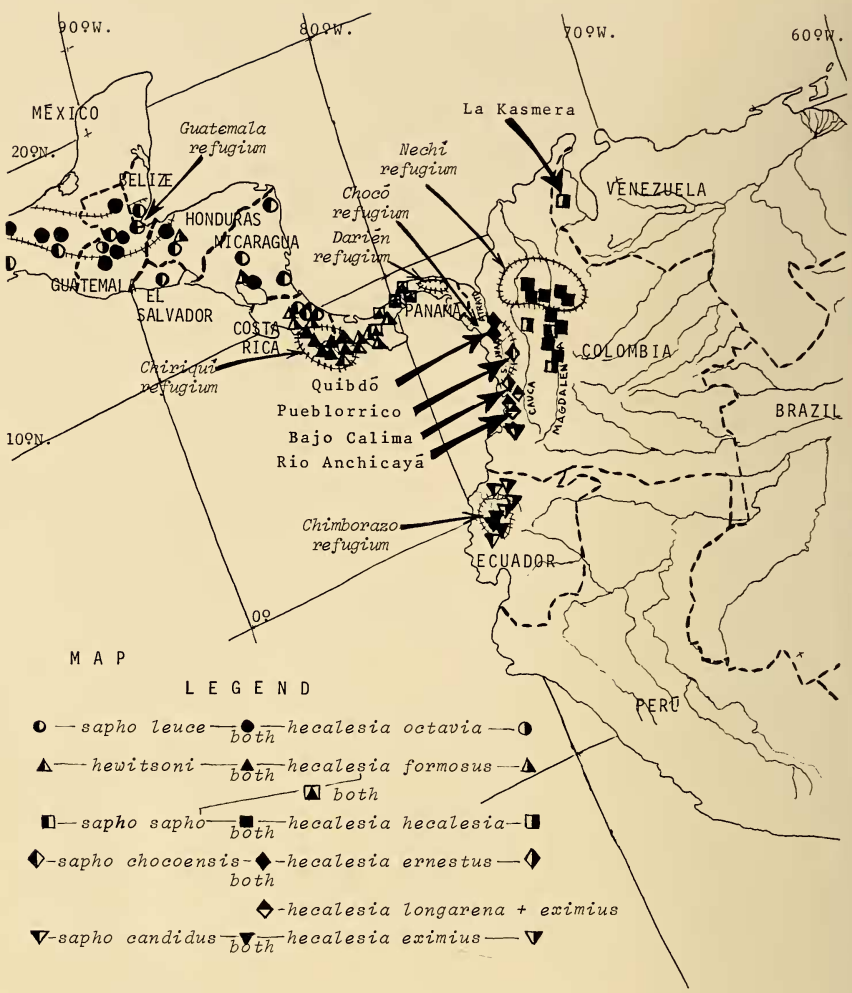
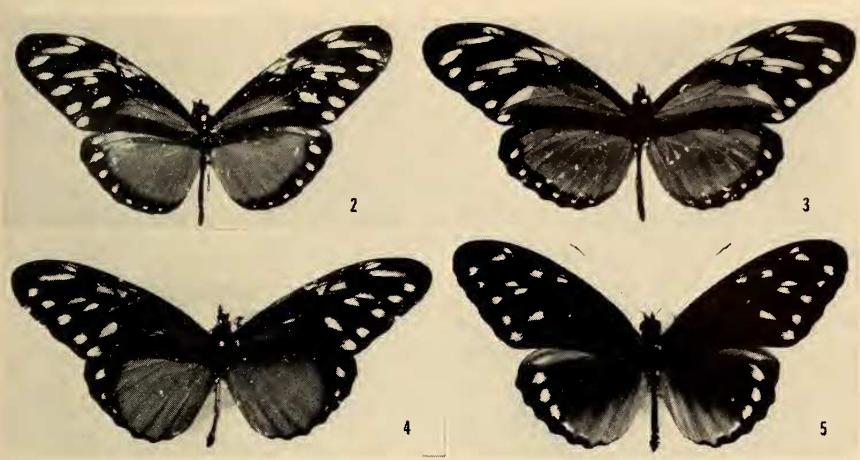


Fig. 1. Distribution map of *Heliconius* species.

River Valley, meeting *H. c. zelinde* Butler from the Pacific slopes and *H. c. cydnides* Staudinger from the upper parts of the western Cordillera and forming spectacularly polymorphic populations (Holzinger & Holzinger, 1968; Brown & Mielke, 1972). *Heliconius eleuchia eleuchia* (Hewitson) also gets across the western Cordillera from the Cauca Valley near Cali and occasionally hybridizes with its Pacific subspecies *H. e. eleusinus* Staudinger in the Anchicayá Valley, giving the named form "ceres" Oberthür (Brown & Mielke, 1972; Brown, 1975).

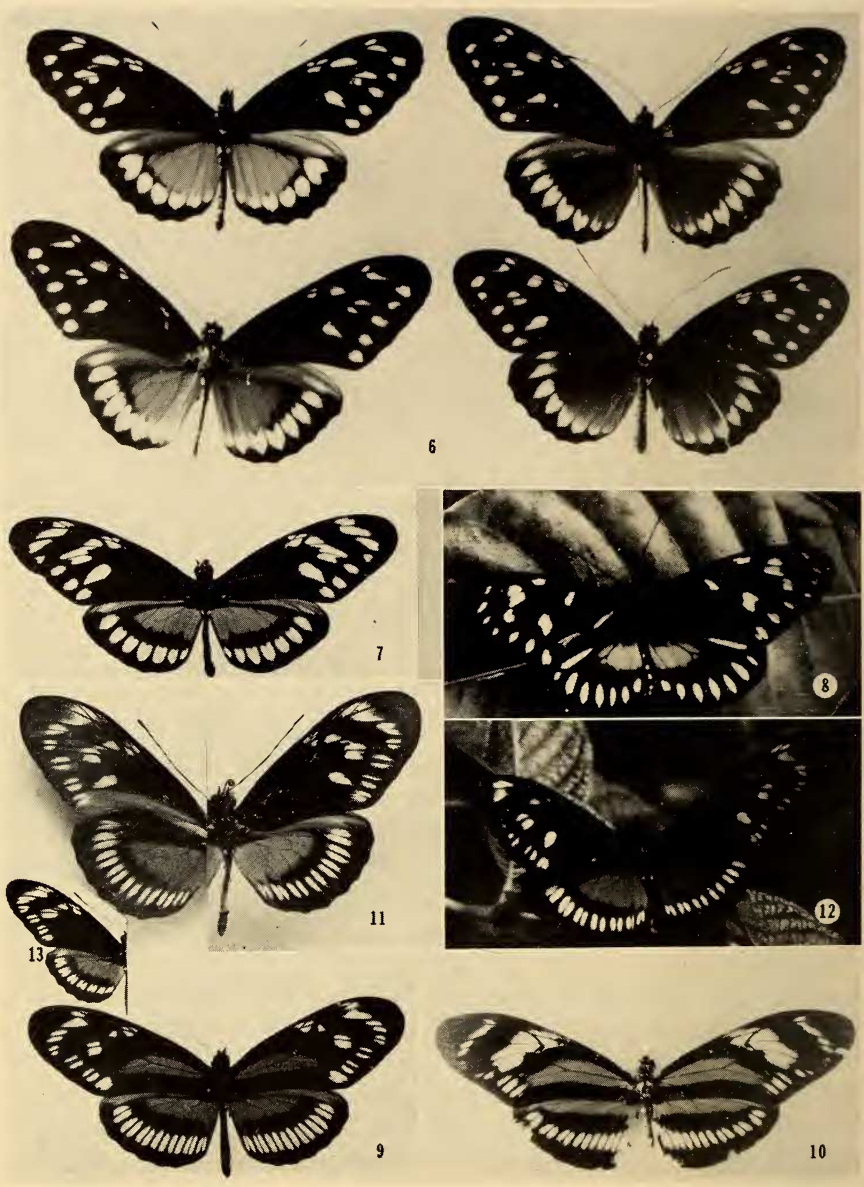


Figs. 2–5. *Heliconius hecalesia.* 2, *H. h. octavia*, male, Panajabel, Chimaltenango, Guatemala (AMNH). 3, *H. h. octavia*, female, Yepocapa, Guatemala (AMNH). 4, *H. h. formosus*, male, Costa Rica? (labelled "Tamahu, Alta Verapaz, Guatemala" but identical to specimens from Costa Rica and Panamá) (AMNH). 5, *H. h. hecalesia*, male, La Kasmera, Sierra Perijá, western Venezuela (Facultad de Agronomia, Maracay). All butterflies ca. 0.70 × life size; black, red-orange or buff and yellow.

Heliconius hecalesia (Hewitson)

Systematics. *Heliconius hecalesia* (Hewitson) and *H. longarena* (Hewitson), a further closely related, allopatric and morphologically differentiated pair of species (Emsley, 1965), might be predicted to meet somewhere in the western part of Colombia and either intergrade or occur sympatrically, depending upon the degree of reproductive isolation associated with their geographic separation and morphological differences. Both are strong flyers that occur from near sea level to over 1500 m altitude and could easily fly over low passes in the western Cordillera. Unfortunately, both are also very local, rare and unusually difficult to locate. Capture of specimens is frequently impossible even when a good colony is discovered, as stops at flowers are very rare and the individuals fly high in near-inaccessible thick forest (even sure identification or analysis of color pattern is thus difficult). Because of these habits of *H. hecalesia* and *H. longarena*, the total number of specimens known, especially for the latter, is very small, and no clear intermediates have been found.

The named subspecies of the two species are few. *H. hecalesia octavia* Bates (Figs. 2–3) is known from southern México to Nicaragua. It is sexually dimorphic, the black and orange male (Fig. 2) converging on



Figs. 6–13. *Heliconius* spp. 6, *H. hecalesia hecalesia* varieties, Colombia: upper left (male), Barranca Bermeja; upper right (male), Bassler's "NE Peru" label = Magdalena Valley, Colombia; lower left (male), Quebrada La Lechera, Rio Opon Region, Quíndio; lower right (female), Quebrada La Borrascosa, same region. Note wide variation in hindwing markings (AMNH). 7, *H. h. gynaesia*, HOLOTYPE, male, "Colombia"?, BM(NH). 8, *H. godmani*, male, in nature, Quibdó, Chocó, Colombia,

Tithorea tarricina duenna Bates, and the light buff-streaked female (Fig. 3) on *Dircenna klugi* (Geyer) (both are common ithomiines in the same region). This phenomenon has only been verified for two other, also very rare species of *Heliconius*: *H. nattereri* C. & R. Felder (Brown, 1970, 1972) and *H. demeter* Staudinger (Brown & Benson, 1975). *H. hecalesia formosus* Bates (Fig. 4) is found in Costa Rica and Panamá; its dark forewing makes it a good member of the common local mimetic group headed up by *Tithorea tarricina pinthias* Godman & Salvin, *Mechanitis polymnia isthmia* Bates (for an explanation of this combination, see Brown, 1976), and *Heliconius hecale zuleika* (Hewitson), though *H. hecalesia formosus* occurs well south of the limits of the latter. From western Venezuela (Brown & Fernández Yépez, in prep.) (Fig. 5) through the Magdalena and lower Cauca valleys of Colombia is found the strikingly patterned *H. hecalesia hecalesia* (Hewitson), converging in color pattern on many local ithomiines such as *Tithorea tarricina tarricina* Hewitson (form "hecalesina" C. & R. Felder) and *Callithomia hezia tridactyla* Hewitson; appreciable variation in size and color of the hindwing markings is known both in *H. h. hecalesia* and its mimics (Fig. 6). A single specimen of unknown collecting locality, *H. h. gynaesia* (Hewitson) (Fig. 7) is so close in color pattern to the endemic Chocó *Heliconius godmani* Staudinger (Fig. 8) and other sympatric ithomiines, that it might be presumed to inhabit the northern Chocó, on the Pacific slope of Colombia. In the southern Chocó is found *H. longarena* (Hewitson) (Fig. 9) with a divided series of postmedian spots and a broad orange mark in the basal area of the forewing. A unique aberration of this entity, lacking all the distal yellow marking on the fore- and hindwings, was captured in the Anchicayá Valley by Leoncito Denhez and sent to H. Gerstner in Germany; its present resting place is unknown. From the Calima and Anchicayá areas southward, generally at moderate elevations, occurs the normal pattern of *longarena* with a broad yellow postmedian band on the forewing, named *eximius* by Stichel in 1923 (Fig. 10). The southern limit presently known for the species in western Ecuador

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January 1972. 9, *H. hecalesia longarena*, HOLOTYPE, male, N. Granada, BM(NH). 10, *H. h. eximius*, male, Rio Palenque Biological Station, near Quevedo, west Ecuador (Allyn Museum of Entomology, Randy Dodson leg.). 11, *H. h. ernestus* nov., HOLOTYPE, male, dorsal (right) and ventral (left) surfaces, Quibdó, BM(NH). 12, *H. h. ernestus* nov., HOLOTYPE, natural pose, shortly after emergence. 13, *H. h. ernestus* nov., PARATYPE, male, Bajo Calima, Valle, Colombia, August 12, 1973, M. Takahashi coll., 0.33 × life size. All butterflies (except as noted) ca. 0.70 × life size; black, yellow and orange.

is Los Rios Province (Rio Palenque Biological Station of the University of Miami, halfway between Santo Domingo and Quevedo).

Field work. The authors first visited Quibdó, in the northern Chocó of Colombia, west of Medellin on the upper Rio Atrato, in the week of 15–21 January 1972. In spite of the high rainfall known for the area (over 10,000 mm per year in the city, the greatest amount known in the world, and unknown but probably appreciably greater amounts in the forested areas farther up the slopes of the Cordillera), most days included several hours of brighter weather, and field work was very productive, especially for little-known endemic forms. On 16 January we were examing a large *Passiflora* (*Tryphostemmatoides*) *gracillima* vine draped over a fence just southeast of Quibdó (Km 2.7 on the road to Itsmina), when we discovered two very strange-looking larvae. They were dirty yellow-green in ground color, with black heads and underparts and a black spot-pattern very similar to most common *Heliconius* larvae (*H. erato* (L.), *H. melpomene* (L.), *H. numata* (Cramer), etc.). Both were in the fifth instar and rapidly completed growth on the same plant, pupating a few days later. The pupa was no less unusual than the larvae, sharing with the pupa of *H. xanthocles* Bates the character of foliaceous projections on the latter abdominal segments (Turner, 1968); it could be rationalized, however, as a streamlined, rather modified version of an *H. erato* chrysalis (Beebe, et al., 1960).

One of the pupae survived, developing into a near perfect adult (lacking one antenna) two weeks later. This specimen (Figs. 11, 12) represented an unknown subspecies of *Heliconius hecalesia* or *H. longarena*, and was indeed transitional between the two, suggesting that they might be but one species. No further larvae were found in later trips to Quibdó, though the vine was still intact and heavily infested with larvae of *Dryas iulia* (F.). No adult *Heliconius hecalesia* were observed flying in the area or in nearby woods, roads and hilltops (the promenading behavior of *H. h. formosus* males in Panamá would suggest a territorial division of ridge, path or hilltop areas).

Since 1972, two additional specimens of this same pattern have been captured: a female was taken near Quibdó, and a male was collected in the lower Rio Calima area, both by Mayuma Takahashi. This new entity apparently represents an undescribed endemic Chocó subspecies of *Heliconius hecalesia*. The unique *H. gynaesia* would then be a transitional form to *H. h. hecalesia*, with fused (not doubled) postmedian elements (note *gynaesia*-like *h. hecalesia* in Fig. 5). The taxon *longarena*, which may still be captured in a limited area west of Cali, would be a transition to *eximius*, possessing an orange cubital bar on the forewing

but still a broken series of yellow spots. A description of this new subspecies is thus presented here.

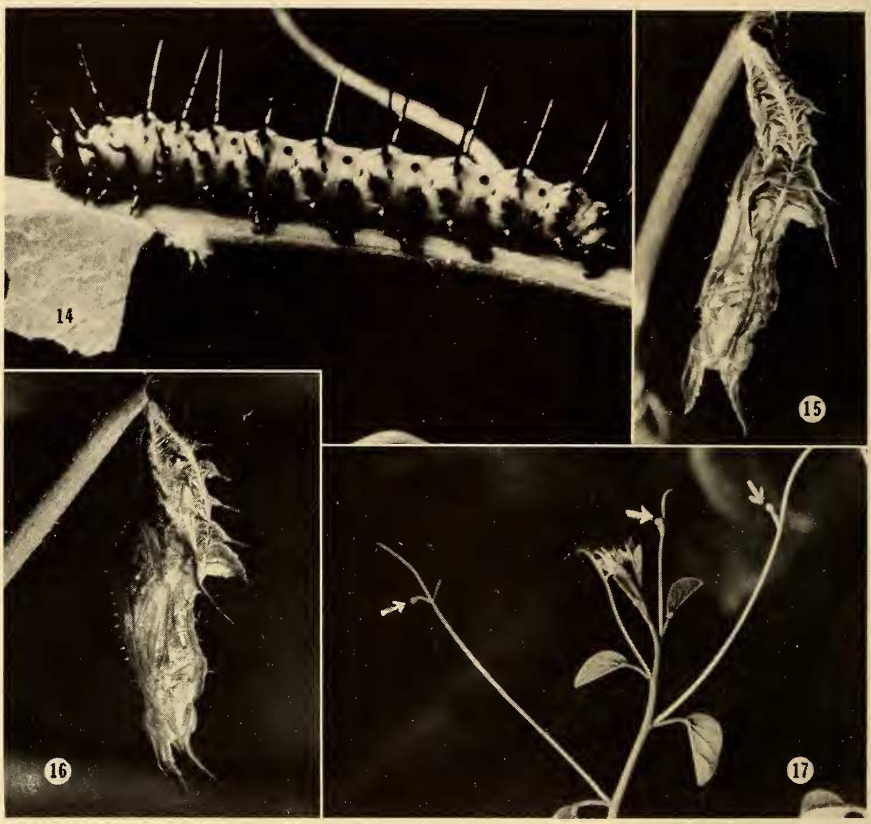
Heliconius hecalesia ernestus K. Brown and Benson, **new subspecies**
(Figs. 11–13)

Male: FW 40 mm. Very similar dorsally to *Heliconius longarena* (Fig. 9), but lacking the bright orange bar over forewing cubitus, base of forewing entirely black; additional yellow spot present in middle of forewing space Cu1–Cu2; hindwing basal orange patch larger, extending distad at veins Cu2 and 2A to meet doubled yellow intervenal submarginal streaks. Similar also to *H. h. gynaesia*, but with all series of postmedian (or submarginal) streaks doubled; forewing yellow markings slightly reduced in area; hindwing orange patch more extensive. Ventral surface essentially identical, with orange costal line margined with yellow on forewing and yellow costal streak fading to orange on hindwing; no red basal spots.

Types. HOLOTYPE: ♂, Quibdó, Chocó, Colombia, reared from larva found on *Passiflora gracillima* vine at Km 2.7 of road to Itsmina, overlooking Rio Atrato SE of city, emerged in Manaus (Amazonas, Brazil) on 4 February 1972, lacking left antenna. Donated by the authors to the British Museum (Natural History). PARATYPES: one ♂, lower Rio Calima (near lower Rio San Juan), 12 August 1973; one ♀, Rio Guayabal, Quibdó, 2 September 1973; both in the collection of M. Takahashi, Shizuoka, Japan.

This subspecies is dedicated to Dr. Ernesto W. Schmidt-Mumm of Bogotá, in gratitude for his many favors, encouragement, hospitality, and specimens of and information about Colombian Heliconiini.

The existence of this color pattern in the north central and in low elevation southern Chocó implies that *hecalesia* and *longarena*, like other related *Heliconius* "species-pairs" separated by the western Cordillera of Colombia, have managed to meet and mix, being best regarded as a single species with *hecalesia* taking name priority. The male paratype, from the south, has a more reduced orange basal area on the hindwing and no yellow cubital spot on the forewing (Fig. 13), which would be expected from its proximity to the *longarena/eximius* mixed populations in the higher parts of the extreme southern Chocó (Alto Rio Calima). The new subspecies is expected to occur sparsely at low or moderate elevations in the western part of Colombia between Quibdó and Buenaventura. The older Hewitson names, both probably transitions from *H. h. ernestus* to the adjacent subspecies, are nonetheless maintained for the time being. They may be applied to the respective phenotypes, even though they possibly do not represent good geographical subspecies. Pure populations of *H. h. longarena* are not known, but the entity is not rare in west central Colombia near Buenaventura at high elevations. Pure populations of *H. h. gynaesia* may someday be found in the extreme northern Chocó, or some part of the Cauca Valley.



Figs. 14–17. *Heliconius hecalesia ernestus* and hostplant. 14, fifth instar larva, Quibdó, Chocó, Colombia, 2× life size, greenish-yellow and black. 15–16, pupa, 1.6× life size, silvery gray. 17, meristem of hostplant (*Passiflora gracillima*) with egg mimics (arrows), Quibdó, Km 2.7 of road to Itsmina, January 1972.

Partial biological information on the new subspecies, *H. h. ernestus*, is also presented here:

Fifth instar larva (Fig. 14). Dark greenish-yellow with black head, legs, scoli, prothoracic plate, prolegs, and anal segment; spot patterned as in *H. erato* larvae. Head scoli 1.0×, dorsal scoli up to 1.3× head height. Mature length about 38 mm. Feeds on *Passiflora gracillima*. Two larvae were found on a single meristem, indicating larval tolerance and possible batch-style oviposition by the female, with larvae semi-gregarious in the early stages and tolerant of others even when large.

Pupa (Figs. 15, 16). Gray, highly sculptured and patterned with fine black and white lines. Reflective patches dorsally on 3TH, 1AB and 2AB. Paired dorsolateral flanges on 3AB (large, directed cephalad), 4AB (smaller, parallel with others), 5AB (very small), 6AB (≅ 4AB) and 7AB (small), each armed with moderately long spine (that on 3AB considerably longer than others). Short spines, arising from

tubercles, also present on 2TH, 3TH, 1AB and 2AB. Tubercles on wing cases in future cells M3–Cu1 and Cu1–Cu2. Antennal cases (on costal margin of forewings) armed with many short spines. Eyes large and prominent. Long, broad, pointed and very slightly serrate paired head appendages. Length about 29 mm; duration 15 days (eight of these at about 18°C, in Bogotá).

The larval foodplant of *Heliconius hecalesia* (*Passiflora gracillima*) shows a most unusual method of probable protection against excessive meristem depredation by *Heliconius* larvae, through egg mimicry (Benson, et al., 1975). The trifid tendrils on meristems develop lateral supernumerary flower buds, which grow rapidly to the size of 1 mm, cease development, and later drop off; these are yellow in color, and their size and shape make them very similar to most *Heliconius* eggs (Fig. 17). It is well known than many species of *Heliconius* assess egg and caterpillar loads in order to avoid multiple oviposition on a single foodplant meristem, because many of the caterpillars are intolerant and even cannibalistic. The best known of these species is *H. erato*, which is frequent in the Chocó. We have found early stages of *H. erato venus* Staudinger on small plants of *P. gracillima* in the Quibdó area. The first author watched an *erato* female inspect carefully and then leave meristems of the Itsmina road *P. gracillima* vine on 17 June 1973 without ovipositing. It is possible that this large plant's abundant fake "eggs" discouraged her. Other *Passiflora* species are known to produce egg mimics as yellow leaf glands and stipule tips, and these may be significant armaments of protection against loss of new vegetative growth to larvae of the physiologically specialized, visually orienting heliconians.

The fact that the *H. hecalesia* larvae in Quibdó were found on a plant bearing abundant egg mimics further supports the hypothesis that *H. hecalesia* uses multiple oviposition and has tolerant larvae because the female apparently did not mind the presence of abundant fake "eggs" on the meristem chosen for an ovipositional site.

However, the use of the *H. hecalesia* foodplant by the solitary and aggressive larvae of *H. erato* (even if often discouraged by egg mimics), suggests that competition may have been an important factor promoting a preference for heavily forested habitats (rarely penetrated by *H. erato*) in *H. hecalesia*, and maintaining its rarity in the present day. A detailed study of possible competition between these two species, prejudicial to *H. hecalesia*, would be easily undertaken in some parts of Panamá or southeastern Costa Rica, where *H. h. formosus* is not uncommon. This would help define the basis for the very large behavioral differences and disparity in abundance between these two systematically very closely related species.

Heliconius sapho Drury

Systematics. The distribution of the subspecies of *Heliconius sapho* Drury, one of the most evolved species in the genus (Emsley, 1965; Brown & Mielke, 1972), would be closely analogous to the pattern of *H. hecalesia* subspecies, were *H. sapho* known from western Colombia. Indeed, the theory of heliconian differentiation in Quaternary forest refugia (Brown, et al., 1974; Brown, 1975) would suggest that similar processes and areas were acting in the evolution and subspeciation of the two species, independent of their geological ages or color patterns.

H. sapho leuce Doubleday occurs in the same area (México to Costa Rica) as *H. hecalesia octavia.* Both presumably evolved in the Guatemala refugium ("Central American Rain Forest"). A splinter species closely related to *H. sapho* (but definitely not conspecific), *H. hewitsoni* Staudinger, probably differentiated along with *H. hecalesia formosus* in isolation in the Chiriquí refugium. The Colombian *H. s. sapho* Drury like *H. h. hecalesia* probably evolved in the Nechí refugium. Like many such entities, it occurs today as far north as central Panamá (where it is barely sympatric with *H. h. formosus* which has spread southward farther than most Chiriquí taxa). The range of *H. hecalesia eximius* in western Ecuador (Chimborazo refugium) is shared by the recently described *H. sapho candidus* Brown which, however, is not known from southwestern Colombia as is *H. h. eximius.* This leaves a fairly large discontinuity in the distribution of *H. sapho*, from the northern Chocó down the coast and in the Cauca Valley, as far south as Nariño. The closest approximation of the superficially similar *H. s. sapho* and *H. s. candidus* is the middle Magdalena Valley in Colombia and Paramba in northwestern Ecuador, some 700 km apart. The recognition of this discontinuity might suggest the existence of a *H. sapho* subspecies in western Colombia, perhaps very rare or even extinct today, but historically predictable as a link in the once continuous distribution pattern of the species. From consideration of the observed close mimetic parallelism of *H. sapho* forms with *H. cydno* subspecies, this hitherto unknown subspecies would be predicted to be blue-black with a single broad white forewing band, much like the endemic west Colombian *H. cydno zelinde* and also the closely related, endemic Chocó *H. eleuchia eleusinus* (formerly placed with *H. sapho*).

Field Work. This predicted but previously undiscovered subspecies of *Heliconius sapho* was encountered by the authors near Quibdó. At Km 204 of the Medellin-Quibdó highway (10 km E of the police check point), a trail into the woods led to a ridge where *H. cydno zelinde* was flying commonly along with a most unusual and mixed population

of *H. sapho.* This consisted of a small number (one of the eleven caught, another seen) of typical central valley *H. s. sapho,* a variety of transitional forms (five captured) with reduced white scaling on the hindwing margin and a majority (five captured, with many more seen) of the expected pattern closely resembling *H. cydno zelinde* with a fully dark hindwing (Fig. 18). As the last form was not present in a pure population, it could not be named, but it was hoped that it could be found pure farther south, in the central Chocó.

A long series of heliconians in the American Museum of Natural History from Itaburi, Pueblorrico on the Pacific slopes of Risaralda Province (formerly part of Caldas), about 80 km SE of Quibdó (Fig. 1), includes many *Heliconius cydno zelinde* (Fig. 19), a number of both white and yellow-banded forms of the similar *H. eleuchia eleusinus* (Fig. 20), and two specimens of the *zelinde*-like *sapho* subspecies. As they may be presumed to come from a pure population, these two are here designated as types of a new subspecies.

Heliconius sapho chocoensis K. Brown and Benson, **new subspecies**

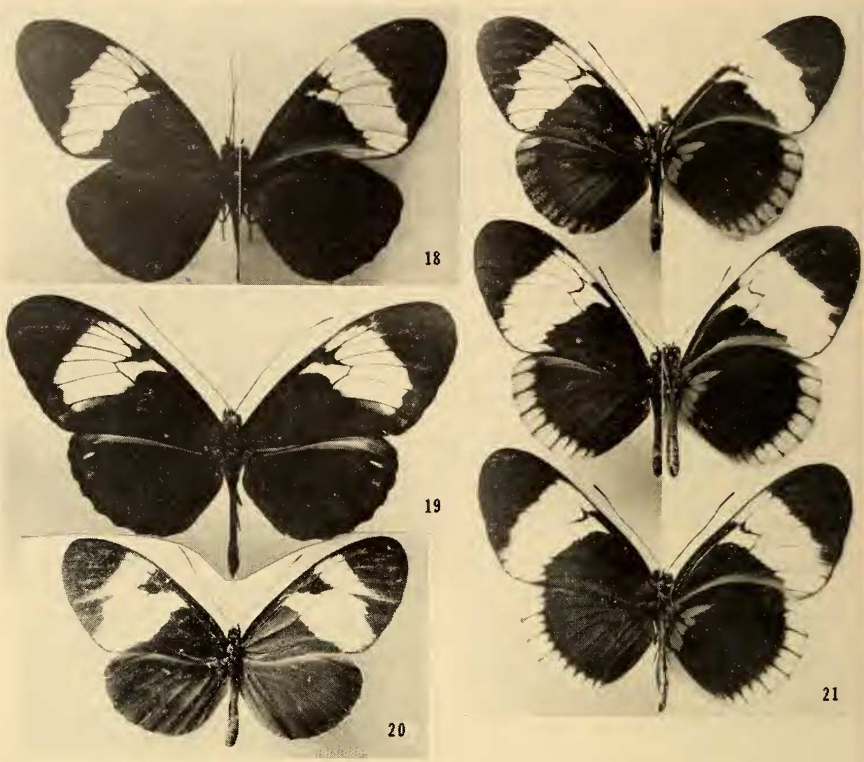
(Fig. 18)

Male. Very similar to the nominate subspecies, but almost entirely lacking white scaling in hindwing border. Forewing dorsally blue-black, divided by broad white postmedian band, crossed by black veins and incised costally at apex of cell to base of vein M3 (leaving a variable element within the cell), slightly tapered anally, conically expanded distally along vein M3. Hindwing dorsally blue-black with very scattered white scales in marginal area. Ventrally similar, black with identical white forewing band, short red costal lines on both wings and five large red basal spots on hindwing which bears almost imperceptible white scaling in submarginal region.

Types. Holotype and paratype in the American Museum of Natural History from Itaburi, "Pueblo Rico," "Caldas" (now Risaralda), Colombia, 1000 m, (5°12′ N, 76°8′ W), January 1946.

A number of similar males and females, not designated as paratypes, were captured in a polymorphic population (Fig. 21) in ridge forest to the south of Km 204, Medellin-Quibdó highway, Chocó, Colombia in January 1972 and June 1973. Most were found either promenading over the ridge or feeding on low white flowers of a cucurbit vine in the early morning. A further polymorphic population of *H. sapho* like that in Fig. 21 was found recently near Cabo Corrientes on the coast west of Quibdó.

The mixed character of the Quibdó *H. sapho* population suggests that some Nechí-refugium forms from the Magdalena and lower (northern) Cauca valleys may be able to cross the western Cordillera either along the Medellin-Quibdó highway (maximum elev. ca. 2000 m) or around the northern spurs of the Cordillera at lower altitudes (perhaps diffusing



Figs. 18–21. *Heliconius* spp. 18, *H. sapho chocoensis* nov., HOLOTYPE, male, Itaburi, Pueblorrico, Risaralda, Colombia, 1000 m, January 1946 (AMNH). 19, *H. cydno zelinde*, Quibdó, Chocó, Colombia, January 1972. 20, *H. eleuchia eleusinus*, Quibdó. 21, Three specimens of *H. sapho* from a mixed population *sapho* × *chocoensis*, Quibdó (Km 204 of highway from Medellin), January 1972. All butterflies ca. 0.70 × life size; blue-black and white with red ventral spots.

south from the Darien area) to meet Chocó forms along the Rio Atrato. That this is indeed possible is supported by the capture of occasional *Heliconius erato* of the *hydara* (Hewitson)-type, with no ventral yellow hindwing bar and reduced or no blue iridescence, in the *H. e. venus* populations near Quibdó, and of *H. cydno* of the *chioneus* Bates type, with a white hindwing border like *H. s. sapho* (occurring in the Nechí area today together with resident *H. c. cydno* (Doubleday), but probably derived from a Darien refugium), in the *H. c. zelinde* populations of the area. Interestingly, however, the *H. eleuchia* of the area occur only as *eleusinus*, even though the two subspecies do meet west of Cali in the Anchicayá Valley far south of Quibdó.

Apparently *H. eleuchia* invades and moves west from the upper Cauca Valley (as does *H. clysonymus*), not inhabited by *H. sapho*, while the latter species moves west from its center in the northern Magdalena and reaches the west coast by a northerly route. The difference is probably related to behavioral or habitat preferences, *H. sapho* preferring lower and less folded terrain and *H. eleuchia* preferring hilly areas. *Hypothyris euclea philetaera* and *Heliconius hecalesia* and *H. cydno*, having more cosmopolitan habitat acceptance, probably follow both these routes of invasion and several more also, in the case of *H. cydno* as two different subspecies.

The distributions of the known subspecies of *H. hecalesia* and *H. sapho* are illustrated in Fig. 1.

It may be predicted that many further new subspecies and missing zoogeographic links will be found in the Chocó, which is a refugium in its own right; a number of these have already been seen in the Ithomiinae.

Acknowledgments

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